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The Thoracic Sclerites and the Systematic Position of Grylloblatta campodeiformis Walker, a Remarkable Annectent, "Orthopteroid" Insect.

By G. C. CRAMPTON, PH.D.*
(Plate XIII)

In the March, 1914, issue of the Canadian Entomologist (Volume xlvi, No. 3, pages 93-99), Dr. E. M. Walker has described and figured a very remarkable insect, Grylloblatta campodeiformis, which combines within itself characters common to a number of "Orthopteroid" insects. Indeed, in many respects, it may be considered as a veritable "living fossil," and from the point of view of the study of insect phylogeny, it is one of the most important of recent pterygotan forms. Through the kindness of Dr. Walker, I have been able to make a study of the external anatomy of this important an-

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nectent insect, and would add the following details to the excellent general description he has already given of it.

In making a comparative morphological study of various insects in connection with the preparation of a paper dealing with the ancestry and affinities of the Hexapoda, it has become apparent that an attempt to trace the genealogy or relationships of insects largely through the study of their wing-venation is of little value. The study of no one structure or organ should be made the basis of such a work; and furthermore, the study of wing venation would be of no value in connection with larval forms, or with aptervgote insects. In addition to this, some of the most important annectent forms (such as Arixenia, Grylloblatta, etc.) have lost their wings, and in such cases, a study of wing-venation would be quite useless. I have therefore laid greater emphasis upon the study of the head and terminal abdominal structures, and the thoracic sclerites (together with the parts of the legs), relegating the wing-venation to a position of secondary importance.

The accompanying figures of the thoracic sclerites of *Grylloblatta*, are of necessity somewhat "diagrammatic," since it was not always possible to clearly distinguish the outlines of the plates in a delicate insect which had been allowed to dry before it was placed in alcohol; and fear of injuring a valuable specimen prevented a thorough examination of parts concealed by overlapping structures. Subsequent examination of specimens preserved in alcohol, however, will, I think, demonstrate that the figures here given, are in the main correct. The terminology here employed, is that used in former papers dealing with the comparative anatomy of the thoracic sclerites (e. g. "Notes on the Thoracic Sclerites of Winged Insects:" *Entomological News*, Vol. xxv, Jan. 1914, pages 15-25).

The thorax of Grylloblatta presents a curious combination of characters also found in the Dermaptera, Isoptera (which are related to the Dermaptera as well as to the Blattids) and Gryllidae. As shown in Pl. XIII, Fig. 1, the outline of the pronotum (pr), mesonotum (mes) and metanotum (met) is quite like that of the nota of such wingless Dermaptera as

Anisolabis; the relative size of the nota is much the same as in Anisolabis, and the anterior sclerite pt (Fig. 1) is apparently also represented in the pronotum of the Dermaptera. The fact that the pronotum (pr, of Fig. 2) does not overlap the pleural region to any extent, while the mesonotum (mes) and metanotum (met) do overlap the pleural region, is strongly suggestive of the condition found in Anisolabis; and, indeed, the dorsal sclerites of Grylloblatta are more nearly like those of wingless Dermaptera than any other insects which I have examined.

The pleural region of the thorax presents some characters suggestive of the Dermaptera, and also of the Gryllids, but on the whole, the pleural region is more like that of the Isoptera than any other insects. The prothoracic episternum (es, Figs. 2 and 3) and epimeron (em) are much like those of the Dermaptera, but the presence of the clearly demarked sclerite bp is a feature which does not occur in any of the pterygote insects which I have studied, and is suggestive of the condition found in apterygote forms. The lateral cervicals (lc, of Figs. 2 and 3) are not divided into a number of smaller plates as in the Dermaptera, but rather resemble those of the Gryllidae, and even slightly resemble those of the Isoptera, except that they do not meet in the mid-ventral line as in the Isoptera and are not subdivided as in the latter insects.

The episterna and epimera (es and em) of the meso- and metathorax are quite like those of the Dermaptera, and are likewise somewhat similar to those of the Isoptera (which also resemble the Dermaptera). The "laterosternite" ls (Figs. 2 and 3) occurs in the mesothorax of the Dermaptera and Gryllidae, but in the metathorax of these insects it is indistinguishably united with the sternal region. Only in the Isoptera is the sclerite ls present as a distinct plate in both meso- and metathorax, as is also the case in Grylloblatta. The shape of the trochantin, tn (Figs. 2 and 3), and its division into an anterior and posterior region by an oblique suture, is characteristic of the Isoptera (and also of the Blattidae, to which the Isoptera are nearly related).

The fact that the sterna are widely separated, is characteristic of the Isoptera; and the triangular outline of the prosternum (bs^1 , Fig. 3) is also strongly suggestive of the Isoptera. The smaller sternal sclerites fs and ss were very hard to distinguish, and I am not certain that their outlines are correctly portrayed, but as far as I could make out, they seem to resemble those of the Isoptera. The larger sternal plate, bs, of the meso- and metathorax is unlike that of any other insect I have examined.

The coxae (Fig. 2, cr) are extremely like those of the Isoptera, save for the fact that the meso- and metathoracic coxae of *Grylloblatta* are not divided by a vertical suture into two parts, as in the Isoptera, and in this respect they are more similar to the meso- and metathoracic coxae of the Blattidae. The trochanters are similar to those of the Isoptera and Blattidae. The femora on the other hand are strikingly similar to those of the Dermaptera. The tibiae also resemble those of the Dermaptera, somewhat, although certain features present in them are suggestive of the Isoptera and Blattidae. The four basal tarsal segments are as much like those of the Blattidae as any, but the terminal tarsal segment is surprisingly like that of the Dermaptera not only in shape but also in the absence of pulvilli, and in the character of the claws it bears.

It is therefore apparent from the study of the thoracic sclerites, that the Grylloblattidae combine in themselves characters which occur in the Dermaptera, Isoptera (and the closely related Blattidae) and Gryllidae. There are also certain features, which "presage" (so to speak) some of the characters which reach a fuller development in the crickets and katy-dids. It would be impossible, however, to form any definite conclusions concerning the affinities of the Grylloblattids from the study of the thoracic structures alone, and it is therefore necessary to take into consideration the head and terminal abdominal structures as well. (The ideal method would be to make a comparative study of the internal structures, the embryological development of the various organs, etc., in addition to the study of the external morphology, but in this case, such an

extended study is impossible, from lack of material). Before attempting to point out the relationship of the Grylloblattidae to the neighboring groups of insects, however, it will be necessary to briefly discuss the systematic position of these related groups, in order to more readily appreciate the meaning of the mutual resemblances of several of these groups, and to realize the significance of the combination of characters found in the annectent Grylloblattidae.

The two groups of pterygote insects which seem to have departed the least from the ancestral type, are the Plecoptera and the Blattidae. Certain Plecoptera nymphs are strikingly similar to the Lepismatidae, not only in their general "habitus," but also in various morphological details, such as the structure of the antennae, mouthparts, prothoracic sclerites, etc.; and in the same way, the Blattidae are strikingly similar to the Lepismatidae. Indeed, the resemblances between these immature Plecoptera (or the Blattidae) and the Lepismatidae are far greater than those between the Plecoptera (or Blattidae) and the higher pterygote insects such as the Diptera, Lepidoptera, etc. It would therefore appear to be very probable that the Plecoptera, Blattidae, and Lepismatidae (i. e. Lepisma, Nicoletia, etc.), are closely related, and doubtless sprang from very similar ancestors (i. e. from ancestors which would doubtless have been grouped into a single order, or possibly a single family).

Very closely related to the Plecoptera, on the one side, are the Embiidae; while on the other, the Plecopteron line of development is very closely paralleled by that of the Dermaptera. Indeed, such forms as Arixenia (specimens of which were kindly loaned me by Dr. K. Jordan), combine in themselves characters found in both Plecoptera and Dermaptera, and the immature stages of such Dermaptera as Dyscritina, Karschiella, Bormansia, etc., in which the forceps are preceded by Plecopteron-like cerci, serve to connect the Plecoptera and Dermaptera—or rather, they indicate a common origin for the two lines of descent.

The character of the antennal segments, the shape of the head, the nature and position of the eyes, the general shape of the mouthparts, many of the thoracic sclerites, certain of the leg structures, and many other features indicate that the Grylloblattids are very closely related to the Dermaptera. Furthermore, the fact that in the immature stages the previously mentioned Dermaptera have segmented cerci (which later become modified to form the forceps) clearly indicates that the Dermaptera are the descendants of forms having segmented cerci similar to those of the Plecoptera. The presence of segmented cerci (which are quite similar to those of immature Karschiella) in the Grylloblattidae, therefore, instead of militating against the view that the Grylloblattidae are closely related to the Dermaptera, would, on the contrary, indicate a community of descent between the two groups; and would simply show that the Grylloblattidae have departed less from the common ancestral type in this respect, than have the Dermaptera—and, indeed, the Grylloblattidae are more "primitive" in many other respects than the Dermaptera are. On the other hand, the presence of a well-developed ovipositor in the Grylloblattidae, might be regarded as a more highly specialized feature (although the fore-runners of ovipositors are to be found in Lepisma, Machilis, and other primitive insects). This however, does not affect the general primitive character of the Grylloblattidae, since it is a matter of common occurrence that animals which are very primitive in some respects, may develop certain other highly specialized features.

The Isoptera have apparently descended from ancestors having segmented cerci also, and, indeed, the cerci of Archoter-mopsis are composed of exactly as many segments as those of Grylloblatta—namely, eight. I had long suspected that the Isoptera were rather closely related to the Dermaptera (as well as to the Blattidae) and upon examining the various structures of Grylloblatta, it at once became apparent that we have in the latter insect a form annectent between the Dermaptera and the Isoptera (and leading to the crickets and katydids). I am convinced that Grylloblatta is descended from an-

cestors very like those of the Isoptera and Dermaptera (with the Plecoptera), and although *Grylloblatta* is much nearer to the Dermaptera than to the Isoptera, it furnishes a "connecting link" between the two. As will be later discussed, *Grylloblatta* also leads us to the common origin of the crickets and katydids.

The Coleoptera also combine certain features found in the Dermaptera and Isoptera, but doubtless are descended from ancestors nearer to the Dermaptera than to the Isoptera. The fact that some beetle larvae have forceps-like terminal abdominal appendages (e. g. Cucujus, Pyrochroa, etc.), while others, such as the Carabidae, have segmented cerci, was for a long time a very puzzling feature in attempting to determine the ancestry of the Coleoptera; but in the light of what has gone before (namely that the forceps of the Dermaptera are merely modifications of the segmented cerci of the ancestral forms) the occurrence of both forceps and segmented cerci in beetle larvae becomes immediately comprehensible, and takes its logical position in the general developmental scheme.

Very closely related to the Isoptera, are the Zoraptera recently described by Silvestri, 1913 ("Descrizione di un nuovo ordine di insetti," Portici, 1913). I have not been able to obtain any of these insects for examination, but it is quite evident that they are very closely related to the Isoptera, and also show certain Coleopterous affinities. Whether they are annectent between the Isoptera and any other group, can only be determined by a closer examination of the thoracic sclerites, etc., which are not clearly shown in Silvestri's figures; but I would not be at all surprised if they should prove to possess characters similar to the Grylloblattidae (and Dermaptera) also.

The Isoptera, as has been previously mentioned, are related to the Grylloblattidae and Dermaptera. They are also closely related to the Blattidae, perhaps more closely than to the Grylloblattidae, and thus occupy a position between the two. The Blattidae, on the other hand, are very closely related to the Mantidae. The complicated interrelations of these various

forms makes it impossible to arrange the orders in a dichotomously branching phylogenetic tree, since such an arrangement does not show the fact that several of the groups may overlap or approach one another from different directions, but merely allows for the branching in one plane.

As was previously mentioned, the Grylloblattidae occupy an intermediate position between the Dermaptera and Isoptera, and apparently branched off at an early stage from the ancestral Dermaptera-Plecopteron group. The tendency toward the development of an ovipositor (present in other primitive insects) has apparently found opportunity for expression in the Grylloblattidae, and in the crickets and katydids, which are descended from ancestors not unlike the Grylloblattidae. Indeed, the terminal abdominal structures of such crickets as Oethancus are strikingly similar to those of Grylloblatta, and the fore-runners of many structures which reach their greater development in the crickets and katydids are clearly evidenced in the Grylloblattidae. The crickets and katydids approach one another in such forms as Gryllacris, and have apparently descended from a common stock. This common stock, in turn, was derived from forms not unlike the Grylloblattidae—in other words, the Grylloblattidae have not greatly changed from the ancestral forms, although they, of course, have developed modifications of their own, as is true of all forms now living.

I have not seen such forms as *Phasmodes, Zaprochilus*, etc., but judging from the figures by Caudell, 1912 ("Orthoptera," family "Locustidae;" *Genera Insectorum*, fascicle 138), *Phasmodes* is an insect allied to the katydids, and related to both Phasmidae and Grylloblattidae. The Phasmidae, on the other hand are related to the Phylliidae (*Phyllium*-like insects), and the latter (Phylliidae) are in reality nothing but greatly flattened, walking grasshoppers!

The line of descent of the grasshoppers ("Acridiidae") is, I think, slightly different from that of the crickets (Gryllidae) and katydids ("Locustidae"), although it closely parallels the latter line. Judging from the antennae, mouthparts, thoracic sclerites, the nature of the "ovipositor," etc., the grasshoppers are in some respects more closely related to the Phylliidae than

to the "Locustidae" and Gryllidae. The fact that the "Acridiidae" Gryllidae and "Locustidae" are all saltatorial should have no great weight, for on this basis, we would have to group together the flea-beetles, Psyllidae, and any other forms which happened to have developed the power of leaping. The saltatorial habit is a purely physiological one, and should not have the weight of a fundamental structural resemblance. as will be elsewhere discussed.

There is apparent in many Phasmids, particularly the tropical forms from India, etc., a marked tendency toward the development of (or the retention of) an ovipositor, and forms such as *Phasmodes* and *Zaprochilus* seem to indicate a rather close relationship between the Gryllid-"Locustid" group (which is an ovipositor-bearing one) and the Phasmidae. On the other hand, forms such as *Timema* (specimens of which were kindly loaned me by Mr. Caudell) seem to point to a relationship between the Phasmidae and the Plecoptera-Dermapteron group, and hence with the Grylloblattidae. The relationship between the Phasmidae and Grylloblattidae, however, is more direct than through the mediation of the Plecoptera-Dermapteron group, and, in all probability, the Phasmidae and Grylloblattidae arose from very similar ancestors.

On the other hand, the Phasmidae and Mantidae are very closely related, and I must confess that the complicated interrelations of these lower groups is a very puzzling feature. Thus some Mantid-like forms such as *Mantoida* are very Neuropteron-like, and even resemble the aberrant Panorpid *Merope*. This, however, may be explained by the fact that the Neuroptera, Plecoptera (Dermaptera, etc.), Mantidae, Phasmidae, etc., all sprang from very similar (closely related) ancestors; and it is therefore to be expected that mutual resemblances would be retained by some members of each group

The Psocidae are regarded by many recent investigators, as very near to the Isoptera and Plecoptera (with the Embiidae)—and therefore to the Grylloblattidae. I do not entirely agree with this view, however. The Neuroptera have departed but little from the ancestral group whence sprung the Trichoptera and Lepidoptera, the Mecoptera, Diptera and Siphonaptera,

and the Hemiptera-Homoptera, and it is with the *Neuroptera* and *Homoptera* that the Psocidae show the closest affinities. It is quite true that the ancestral Neuroptera very closely approach the ancestral Plecoptera, and in this way the Psocidae would be related to the Plecoptera and Isoptera, but the relationship is a rather indirect one, and, as has been stated, the affinities of the Psocidae are rather with the Homoptera and Neuroptera, than with the Plecoptera and Isoptera.

The complicated inter-relations of the various orders of insects makes it extremely difficult to arrange them in clearly defined groups. There are, however, at least two clearly defined "nuclei," or centers, about which the majority of pterygotan insects group themselves; further investigation will doubtless disclose other such centers. The two centers in question are the Neuroptera and the Plecoptera, and the ancestors of both of these groups were, in all probability, derived from forebears similar enough to be grouped into a single family.

The insects which group themselves about the "Neuropteroncenter" constitute a supersection which may be referred to as the Neuropteradelphia (or "Neuropteron-brotherhood"), and all are the descendants of very similar ancestors—i. e., their ancestors would have been grouped into a single family. Here belong the following orders: Neuroptera, Trichoptera, Lepidoptera, Mecoptera (Panorpidae), Diptera, Siphonaptera, Homoptera, Heteroptera. Clinoptera (Psocidae), and others.

The insects which group themselves about the "Plecopteroncenter" constitute a second supersection which may be referred to as the **Plecopteradelphia** (or "Plecopteron-brotherhood"), and all are the descendants of very similar ancestors. Here belong the following orders: Plecoptera, Platyptera (restricted to the Embiid-like insects), Dermaptera, Notoptera (Grylloblattid-like forms), Zoraptera, Isoptera, Cheleutoptera (Phasmid-like forms), Phylloptera (*Phyllium*-like forms), Diphtheroptera (grasshopper-like forms), Orthoptera ("Locustidae" and Gryllidae), and others.

The orders Palaeoptera (Blattid-like forms) and Dictyoptera (restricted to the Mantid-like forms) are very closely

allied, and may possibly be grouped into a third supersection, the Palaeopteradelphia. I am inclined, however, to include them in the Plecopteron group, since the Blattidae are closely related to the Isoptera, and also resemble certain Plecopteron nymphs.

Many pterygotan orders of doubtful origin (such as the Hymenoptera, Mallophaga, etc.) have been omitted from the foregoing discussion. It may be remarked, however, that the Hymenoptera very probably arose from ancestors not very unlike those of the Isoptera and Notoptera (Grylloblattidae), and would therefore be included in the Plecopteron group. This point, however, can be decided only after a more extended study of the Hymenoptera, and an examination of intermediate forms not at present accessible.

It will be noted in the foregoing discussion, that the Grylloblattidae are grouped into a distinct order, the **Notoptera** (a term signifying that the wings have been superseded by prolongations of the notum), and this, I think, is fully justifiable, if such groups as the Isoptera, Dermaptera, etc., are also to be considered as distinct orders. In no other group of insects do we find a combination of segmented cerci, ovipositor, broad coxae, five-segmented tarsi, divided trochantin, laterosternite (plate *ls*, of Figs. 2 and 3), distinctive sterna, etc., etc., which is characteristic of the "Notoptera," and clearly demarks the order from all others.

It will also be noted that the *Phyllium*-like insects have been grouped into a separate order, the **Phylloptera**. (or "leaf-winged" insects). These are differentiated from other insects by the flattened condition of the body, together with the great reduction of the hind wings, the reduced and flattened antennae, the broad sternites, with peculiar pleural sclerites somewhat resembling those of the grasshoppers (yet are folded upward and "mesal-ward" in a distinctively characteristic fashion), the greatly reduced "cerci," flattened and greatly modified "ovipositor," etc.

The Phasmid-like forms and the Phylliidae are usually grouped by recent investigators, into a single order termed the

Phasmoidea. I quite agree with Shipley, 1904 ("The Orders of Insects," Zool. Anz., Vol. 27, pp. 259-262), however, in his contention that the terms applied to the orders of pterygote insects should always end in "-ptera," for the sake of uniformity. Since the term Phasmoidea does not end in "ptera," I would substitute for it the designation Cheleutoptera (referring to the folding of the hind wings in longitudinal plaits, when at rest), and would also remove the Phylliidae from the "Phasmoidea," and place them in a separate order, the Phylloptera.

The grasshoppers differ from the remainder of the "Saltatoria" in that the ovipositor is short, the cerci are greatly reduced, the sterna of the meso- and metathorax instead of being separate, are closely united and interlock (or are "dove-tailed") in a peculiar fashion, there is no plate (the laterosternite) between the mesothoracic sternum and pleural region as in the other forms, a single pulvillus (absent in the other forms) occurs between the tarsal claws, the labium and other mouthparts are different from those of the other forms, as is true of the antennae (which are short, and have segments of a different character), etc., etc. I have therefore placed the grasshoppers in a different order, which I would call the **Diphtheroptera** (or "leather-wings," referring to the nature of the tegmina).

The crickets and katydids form the greater part of the order "Orthoptera" (in the restricted sense), and compose its two principal suborders. The crickets form a distinct suborder, the Gonioptera (so-called from the fact that the lateral portion of the tegmina is bent downward and forms an angle with the upper portion of the tegmina); and the katydids form another well-defined group, which may be called the Phytoptera (from the resemblance of the wings to parts of the plants). The Gryllotalpidae possibly form another suborder, the Paraphytoptera, intermediate between the other two; but this point needs further investigation. The Phasmodes-like forms are sufficiently different from the other katydids to form a distinct suborder—if not a distinct order; which may be designated as the Protophytoptera.

The Blattidae and Mantidae are classed as distinct orders by certain recent investigators (Handlirsch, etc.) and very rightly so, but the terms Blattoidea and Mantoidea, applied to these orders, do not end in "-ptera," as they should do, for the sake of uniformity. I would therefore substitute for "Blattoidea," the designation Palaeoptera (referring to the ancient character of the wings), and for Mantoidea, I would substitute the older designation Dictyoptera (used in the restricted sense).

The Hemimeridae are regarded by some investigators as related to the Blattidae, but Verhoeff has correctly classed them with the Dermaptera, and regards them as a suborder, to which he applies the designation Dermodermaptera. The Arixenidae are also to be regarded as aberrant Dermaptera, and form a suborder which may be called the **Plecodermaptera**, from their resemblance to the Plecoptera.

SUMMARY.

The principal points brought out in the foregoing discussion may be briefly summarized as follows:

- (1) The thoracic structures of the Grylloblattidae present a combination of characters found in the Dermaptera, Isoptera and Gryllidae.
- (2) The Grylloblattidae constitute a distinct order, the Notoptera.
- (3) The Notoptera occupy a position intermediate between the Dermaptera and Isoptera, and are the nearest living representatives of the common ancestors of the Gryllidae and "Locustidae" (Tettigonidae).
- (4) The Platyptera (Embiidae), Plecoptera, Notoptera and Dermaptera are very closely related, and sprang from ancestors so similar that they would have been grouped in a single family, or subfamily.
- (5) There are at least two (possibly more) centers about which pterygote insects group themselves, namely, the Plecoptera and the Neuroptera. The ancestors of both probably sprang from a common stock.

(6) The Plecoptera (certain immature forms) and Palaeoptera (Blattidae) are strikingly similar to the Lepismatidae, and the ancestors of all three must have been very closely related.

EXPLANATION OF PLATE XIII.

- Fig. 1. Terga of pro-, meso- and metathorax and first abdominal segment, seen from above.
- Fig. 2. Lateral view of anterior portion of the insect. Only the basal portion of the abdomen is shown (as dotted lines). The position of the episternum and epimeron (of meso- and metathorax) indicated by dotted lines, to indicate that they lie below the overlapping terga.

Fig. 3. Ventral view, showing sternal plates and one side of the body.

All are represented as though stretched out in one plane.

All figures are of Grylloblatta campodeiformis E. M. Walker. The figures are somewhat diagrammatic.

Abbreviations.

1-a—First abdominal tergite. mes-Mesonotum. met-Metanotum. bb-Basal pleural sclerite. br-Pronotum. bs—Basisternite (largest sternite). pt-Pretergite. cx-Coxa. cm—Epimeron. s—Spiracle. ss—Spinasternite. es-Episternum. ta-Tarsus. fe—Femur. fs-Furcasternite (in two parts ti-Tibia. tn-Trochantin. in prothorax). lc-Lateral cervical sclerites. tr-Trochanter. ls-Laterosternite.

The subscripts 1, 2 and 3 indicate that the structure in question belongs to the pro-, meso- or metathorax.

Two New Names in the Ascalaphidae (Neur.)

The genus Ptynx Lefev. was proposed with costatus Burm. as only species; this species was already the type of Haploglenius, so that Ptynx Lefev. is a synonym of Haploglenius. Necroptynx McClend. was proposed to replace Ptynx (preoc.), and so also falls as synonym of Haploglenius. Therefore, I propose Ascaloptynx n. n. with the generic characters assigned by Weele for Neuroptynx, with Ascalaphus appendiculatus Latr. as its type.

The genus Orphnc Lefev. (Agassiz gives Orphnus also preoc.) was proposed for Ascalaphus appendiculatus, but is preoccupied by Hübner. Orphnc as used by MacLachlan and Van der Weele is thus without a name, and MacLachlan was aware that he was using the name in a wrong sense. Therefore, I propose Ascalorphne n. n. with the generic characters usually assigned to Orphne, and with Ascalaphus macrocercus Burm. as its type.—Nathan Banks, East Falls Church, Virginia.